

# On the Surface Swarming of Euphausiid Crustaceans<sup>1</sup>

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**ABSTRACT:** A general aspect of the daytime surface swarming of *Euphausia pacifica* in Japanese nearshore waters is described in connection with the water temperature. Swarming usually starts with a local minimum temperature around 7°C and terminates with a temperature just below 16°C. The swarming season is essentially in spring, from February through May, with little difference among regions. The main swarming areas are on the Pacific coast around Kinkazan, and on the coast of the Sea of Japan around Sadogashima, in Wakasawan and its vicinity, around Oki, and on the east side of the Tsushima Gunto.

It is shown that the swarming is closely related to cold water masses, and that the approach of offshore cold water masses to the nearshore areas and the mixing process in the coastal areas may provide favorable conditions for swarming. Swarming of *E. pacifica* is a phenomenon that occurs at the margins of the cold water bodies, and is related to the seasonal change in the geographical distribution of those euphausiids.

A uniformly low water temperature profile must be the necessary condition for swarming, but other possible factors stimulating euphausiids to swarm are enumerated.

IT HAS BEEN REPORTED frequently from various parts of the world that conspicuous daytime aggregation of euphausiids takes place at the surface in rather nearshore waters (Table 1). The animals swarm in such large numbers that the sea surface turns red or brownish-red from their red and/or orange pigments. This phenomenon, as Bigelow (1926) pointed out, differs from their usual vertical migratory behavior because it occurs in the daytime, independent of the light intensity.

Most previous reports on this peculiar behavior of euphausiids have been descriptive, and very few observations have been made on its relationship to environmental factors. This may be attributed not only to the complexity of animal behavior in general, but also to the capriciousness of such phenomena. As is the

case with red tides, the surface swarming of euphausiids is not predictable from physical measurements.

Such a swarming phenomenon with *Euphausia pacifica* occurs in the nearshore waters surrounding Japan. A fishery based on *E. pacifica* is maintained in certain areas—around Kinkazan (Komaki, 1957), in Wakasawan Bay and vicinity, and along the coast of northwestern Kyushu. The local fishermen scoop *E. pacifica* swarming at the surface with a pyramid-shaped net. The surface swarming of euphausiids is regarded as sporadic, but the existence of the euphausiid fishery means that the surface swarming of *E. pacifica* must be at least an ordinary annual phenomenon.

While participating in the Survey of the Warm Tsushima Current and Related Waters during the period from 1953 to 1958, the author carried out ecological studies on euphausiids and reported briefly on the relationship between water temperature and the swarming of *E. pacifica* (Komaki and Matsue, 1958). The present paper emphasizes this relationship more extensively, employing additional data, information, and references.

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TABLE 1  
REPRESENTATIVE REPORTS ON EUPHAUSIID SWARMING

REFERENCE	SPECIES*	REGION	SEASON
Smith (1879)	<i>M. norvegica</i>	Eastport area	autumn
Murray (1888)	<i>M. norvegica</i>	Loch Fyne, Scotland	
H. F. Moore (1898)	<i>Thysanopoda</i> spp.	Eastport area	summer, fall
Lo Bianco (1902)	<i>M. norvegica</i>	around Capri I.	Feb., June, July 1901
Bigelow (1926)	<i>M. norvegica</i> <i>T. raschii</i> <i>T. inermis</i>	Gulf of Maine	spring-fall
MacDonald (1927)	<i>M. norvegica</i>	Oslo Fjord	fall, early winter
Hjord and Ruud (1929)	<i>M. norvegica</i>	off Møre, Norway	spring-fall
Hardy and Gunther (1935)	<i>E. superba</i>	S. Georgia waters	Nov.-Feb.
Fish and Johnson (1937)	<i>Thysanoëssa</i> spp.	Bay of Fundy	
Manteufel (1938, 1941)	<i>T. inermis</i>	Barents Sea	winter-spring
Mossentzova (1939)		Barents Sea	spring
Dakin and Colefax (1940)	<i>N. australis</i>	Sydney area	Sept. 1938
Einarsson (1945)	<i>M. norvegica</i> <i>Thysanoëssa</i> spp.	N. Atlantic	spring-summer
Gunther (1949)	<i>E. superba</i>	S. Georgia waters	Jan. 1937
Uda (1952)	<i>E. pacifica</i>	southern part of Sea of Japan	Feb.-May 1948
Sheard (1953)	<i>N. australis</i> <i>T. gregaria</i>	S. Australia, Bass Strait, S. Victoria, N. Tasmania waters	breeding season
Fisher et al. (1953)	<i>M. norvegica</i>	Monaco coasts	Aug. 1951 Jan. 1952
Boden et al. (1955)	<i>T. spinifera</i>	La Jolla coasts	June 1948
Peters (1955)	<i>E. superba</i>	Bouvet area in Antarctic waters	December
Komaki (1957)	<i>E. pacifica</i>	around Kinkazan	Feb.-May
Komaki and Matsue (1958)	<i>E. pacifica</i>	Japanese waters	Feb.-May
Ponomareva (1955, 1959, 1963)	<i>T. longipes</i> <i>T. inermis</i> <i>T. raschii</i> <i>E. pacifica</i>	northern part of Sea of Japan, N. Pacific	Mar.-June
Zelickman (1961)	<i>T. inermis</i> <i>T. raschii</i>	Murman coasts	Mar.-July
Brinton (1962b)	<i>E. pacifica</i>	north of Pt. Conception	Apr. 1956
Marr (1962)†	<i>E. superba</i>	S. Georgia waters	

\* Abbreviations of genus names: *E.* = *Euphausia*, *M.* = *Meganyctiphanes*, *N.* = *Nyctiphanes*, *T.* = *Thysanoëssa*.

† Review of surface swarming of *E. superba* in Antarctic waters.

#### SOURCES OF INFORMATION

##### Swarming

Because of the infrequency of swarming of euphausiids in the Sea of Japan since 1953, direct observation of the phenomenon was not possible, but valuable information on the local

swarming of euphausiids was obtained from fishermen. Fishermen are the best, most frequent, and most experienced observers of phenomena occurring in their favorite fishing grounds. From 1954 to 1956, a questionnaire was sent three times to more than 800 local fishermen's unions, which are scattered along

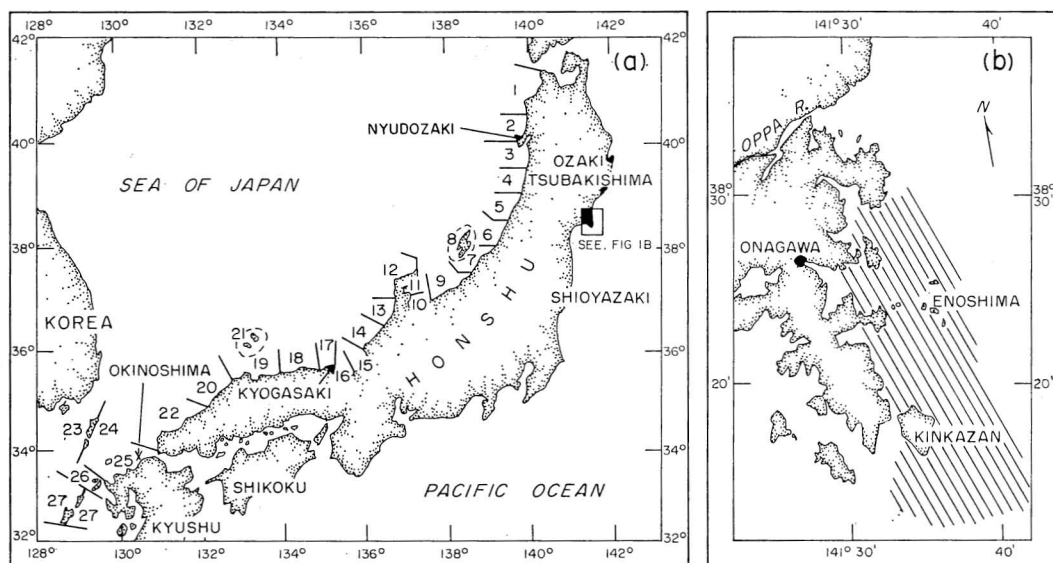


FIG. 1. (a), Map showing partition of coastal areas of the Sea of Japan into 27 zones in order to observe the regional differences in euphausiid swarming. Zones 15 and 16 cover the Wakasawan area. (b), Fishing ground (shaded area) of *Euphausia pacifica* in the vicinity of Kinkazan.

the coasts of Honshu, Kyushu, and adjoining small islands facing the Sea of Japan.

The rate of response to the questionnaire was approximately 30%. To facilitate analysis of the replies, the coastline of the Sea of Japan was partitioned into 27 zones of  $0.5^\circ$  latitude or according to geographical features of the coasts (Fig. 1a). The fishermen's unions were divided into 27 groups corresponding to these zones, so that geographical differences in the swarming, if any, could be detected. There were many responses suggesting interesting relationships between the swarming and environmental factors (hydrographical, meteorological, biological, and so on). The author interviewed fishermen from important regions, on the basis of the results of the questionnaire, such as the Wakasawan area. Information that could be treated numerically (at least to some extent) was employed in the present paper.

It was learned that, along the Pacific coast, the area around Kinkazan (Fig. 1b) is the only place where the relatively stationary swarming is observed every year and the euphausiid fishery is maintained. The author visited this area in every swarming season and participated in the euphausiid fishing operation in order to make direct observations. No written question-

naires were employed there. Reliable quantitative records of euphausiids fished from the Kinkazan district since 1953 were obtained from the fish market in Onagawa where almost all the euphausiids from this fishing ground were landed, but no similar numerical data on the yield of euphausiids were available from the Sea of Japan.

#### Water Temperature

Among the important environmental factors governing distribution and behavior of the organisms, water temperature is not only the most important factor, but also is the one for which data can be obtained most easily. Accordingly, these data were sought from the files of the hydrometeorological observations made by the various maritime and fisheries agencies listed below:

- Federation of Fishermen's Unions of Miyagi Prefecture, Onagawa Branch. 1953–1959. Fisheries Statistics.
- Fukushima Prefecture, Fisheries Experimental Station. 1956. Data on oceanographic observations off Fukushima Prefecture, 1914–1939.
- Imperial Fisheries Research Office, Central Laboratory. 1915–1950. Data on oceanographic surveys in the surrounding areas of Japan.
- Iwate Prefecture, Fisheries Experimental Station.

1954-1956. Data on oceanographic observations off Iwate Prefecture.  
 Japan Sea Regional Fisheries Research Laboratory.  
 1953-1959. Monthly report on the out-lined sea conditions of the Sea of Japan.  
 Ministry of Agriculture and Forestry, Section of Statistics. 1946-1956. Fisheries Statistics.  
 Miyagi Prefecture, Fisheries Experimental Station.  
 1910-1959. Records of hydrometeorological observations at Enoshima, Miyagi Prefecture.

### *Plankton Samples Collected in the Sea of Japan*

Thousands of plankton samples were collected during the period 1953-1958 by various institutions that participated in the Survey of the Warm Tsushima Current and Related Waters. Most samples were collected in a strip within 100 miles of the coastline. The selected samples were examined for the purpose of ecological studies on euphausiids, and they were very useful in the confirmation of euphausiid species composing surface swarms.

## RESULTS

### *The Species*

Examination of specimens landed at the Onagawa fish market revealed that the euphausiids swarming in the Kinkazan waters were large specimens of *Euphausia pacifica* (longer than 20 mm from the tip of the rostrum to the end of the telson). Throughout four fishing seasons, only one stray specimen of *Nematoscelis difficilis* was found among the catches of huge quantities of *E. pacifica*. Combined swarmings of more than two species, such as those reported by H. F. Moore (1898), Fish and Johnson (1937), and Zelickman (1961), were not encountered in the Kinkazan waters.

The following five species of euphausiids inhabit the Sea of Japan (Ponomareva, 1955; Komaki and Matsue, 1958): *E. pacifica*, *Thysanoëssa raschii*, *T. inermis*, *T. longipes*, and *Pseudeuphausia latifrons*.

Plankton samples collected during the survey showed that *E. pacifica* and *P. latifrons* could be obtained from the areas within 100 miles from the coast. *Thysanoëssa* spp. never have been collected from that area, although Ponomareva (1959, 1963) has reported that the three *Thysanoëssa* species mentioned appear at the surface, forming remarkably dense

swarms in the northernmost part of the Sea of Japan. *P. latifrons* is a small, warm-water form, shorter than 10 mm in total length (Hansen, 1916; Brinton, 1962a), and apparently it penetrates into the southernmost part of the Sea of Japan from the Tsushima Kaikyo only during summer and fall (Komaki and Matsue, 1958). Samples from surface swarms of a few occasions revealed that the swarms were composed of large *E. pacifica* only. Thus, *E. pacifica* must be the species composing the surface swarms in the nearshore waters of the Sea of Japan.

### *Features of Swarming*

Hardy and Gunther (1935) have described beautifully the swarming behavior of *E. superba* at the surface, and their descriptions can be exactly applied to the surface patches of *E. pacifica*. The animals swim as close as 1-2 cm from each other, orienting themselves in one direction as if commanded by a leader. The swarms look like formless clouds, and frequently change in shape. They are red, brownish-red, or pale brown in color, depending upon their distance from the surface.

When participating in euphausiid fishing operations in the Kinkazan waters, the author found that swarming took place intensively at intervals of a few days. As shown in Figure 2, the daily landings of *E. pacifica* at the Onagawa fish market fluctuate with a pulselike rhythm. Inasmuch as only surface patches of euphausiids are harvested because of the fishing method, the landing on a given day is probably related to the standing crop of euphausiids swarming at the surface on that day. Daily catch per unit of fishing effort is the most suitable term to use in discussing such a fluctuation of standing crop, but data indicating fishing effort were not available. Fishing boats unload their catches at the market two or three times a day while euphausiids are abundant. Accordingly, the aggregate numbers of fishing boats in Figure 2 change approximately in parallel with the landings of euphausiids.

Efforts were made to relate this pulselike occurrence of swarming to the environmental factors that vary within short periods, e.g., irradiation, wind direction and intensity, and

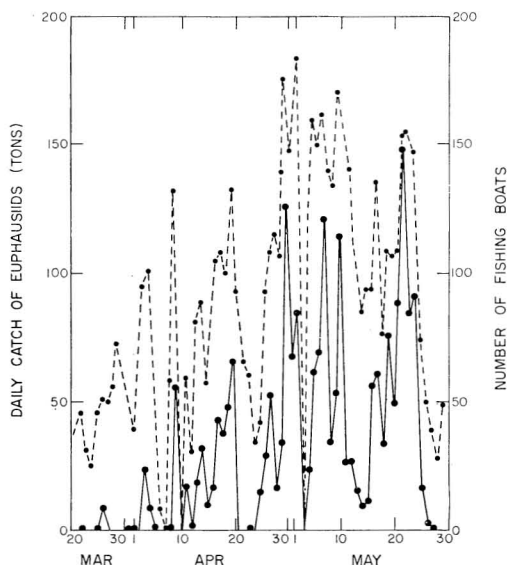


FIG. 2. Daily landings of *Euphausia pacifica* (solid line) from Kinkazan waters and daily change of aggregate number of fishing boats (dashed line) yielding euphausiids (1959).

the like, but there were no apparent relationships. The yield on a calm day is likely to be more abundant than that on a rough day, but this is caused essentially by the relative difficulty of the fishing operation. The time of swarming throughout a given day is not definite. It occurs in early morning on some days, while on other days it takes place in the afternoon even in bright sunshine.

#### Swarming Season

The fishing season of euphausiids corresponds with the swarming season in the area where the euphausiid fishery is carried out. As shown in Figure 2, the swarming season during 1959 in the Kinkazan waters started in the middle of March and terminated at the end of May. The season, however, changes slightly from year to year. The swarming season in the Kinkazan waters ranges between late February and late May in maximum extent.

Figure 3 shows the general aspect of the swarming season along the coasts of the Sea of Japan. The rectangles in Figure 3 show the range of the swarming season in the zones indicated by the numbers in Figure 1a. Figure 3 was derived from replies of fishermen to the

question, "In what month(s) do you *usually* observe the euphausiid swarming in your favorite fishing grounds?" The three degrees of swarming intensity of euphausiids were fixed as follows: 1–3 affirmative response(s) from a certain zone in a given month were expressed by a white area, 4–6 affirmative responses by a shaded area, and more than 7 by a black area. Actually, each month expressed by a black area represents more than 15 affirmative responses.

Figure 3 also indicates that the major swarming regions in the coastal areas of the Sea of Japan are around Sadogashima (zone 8), in Wakasawan and vicinity (zones 15 and 16), off Sanin district including Oki (zones 18–21), and on the east side of the Tsushima Gunto (zone 24).

There seems to be a tendency for swarming to take place earlier in the year in the southern part of the Sea of Japan. Thus, in the north of Kyushu (zones 23–25), the most intensive swarming is observed in February and March; in the Wakasawan and Sanin districts (zones 15–21), the most notable swarming season is in March and April (also in May in some zones); and in the area surrounding Sadogashima (zone 8), the euphausiids aggregate most actively in April through June. According to the fishermen's information, the swarming season in each zone changes from year to year, as in the Kinkazan waters. The beginning, peak, and terminating times of the swarming are different from year to year. The swarming season along the coasts of the Sea of Japan occurs between January and June.

#### Seasonal Change of Water Temperature

Figure 4 shows the mean surface temperature and salinity cycles throughout a year at three representatives coastal points in the Sea of Japan. All temperature records for a given month, taken over a period of 26 years, were averaged. The same was done with salinity determinations.

Upon comparing Figure 4 with Figure 3, it may be seen that the occurrence of swarming is closely associated with colder water temperatures. Swarming starts at a slightly higher temperature than the local minimum, continues with increasing temperature, and then terminates as the temperature exceeds 16°C. The

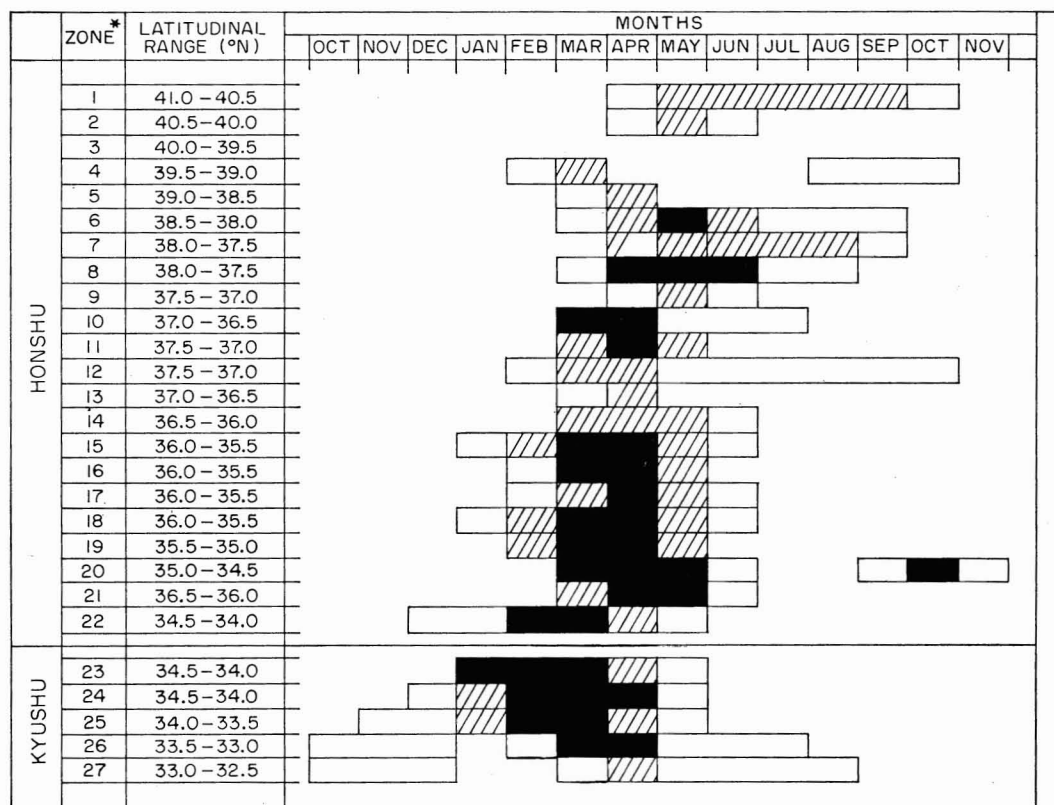


FIG. 3. Swarming season of *Euphausia pacifica* in the coastal areas of the Sea of Japan (see text). Zones are shown in Figure 1a.

temperature during the swarming season ranges between 7° and 16°C.

Figure 5a shows the average change of surface water temperature during the first six months at Enoshima, a tiny island located in the middle of the fishing ground for euphausiids around Kinkazan (Fig. 1b). Daily hydro-meteorological observations have been made at this island since 1910, with an interruption during the period from 1945 to 1953. In this Pacific coastal region, swarming starts with the minimum surface water temperature (in February and March), continues as the temperature rises, and ends when it reaches about 12°C, thus demonstrating again a relationship between swarming and low temperature.

The vertical distribution of temperature and its annual change was also examined for the Kinkazan waters. Figure 6 shows the mean annual changes of temperature profiles down to 200 m at two points 10 miles off Ozaki (a)

and Shioyazaki (b), respectively. It was not possible to learn the results of long-term oceanographic observations carried out at a definite station adequately close to Kinkazan, which would have been an ideal station. Therefore these two stations were substituted. Monthly observations have been made along the west-east lines, including the above two stations as the nearest ones to the coast, for 20 years off Ozaki and for 24 years off Shioyazaki. Figure 6 shows that sea water is completely mixed from the top down to a depth of 200 m, and that a low temperature prevails during the months corresponding to the swarming season of euphausiids.

It seems probable that the water temperature profile in the euphausiid fishing ground near Kinkazan is more nearly similar to that off Ozaki than to that off Shioyazaki, which is located in the south where the sea conditions are more directly influenced by the warm

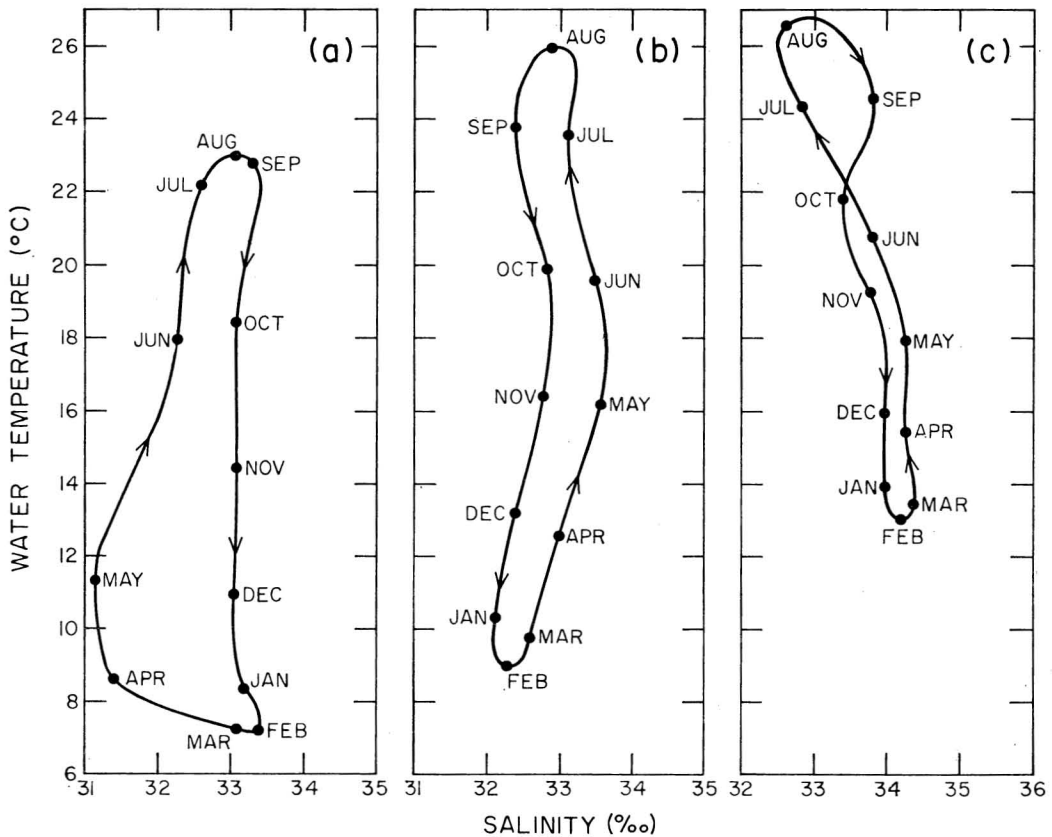


FIG. 4. Annual changes of surface water temperature and salinity at Nyudozaki (a), Kyogasaki (b), and Okinoshima (c). Locations are shown in Figure 1a. Measurements were made from 1915 to 1950 with interruptions in some years.

Kuroshio. Such a condition of low and uniform temperature as prevails from the surface down to 200 m in the vicinity of Kinkazan provides no temperature barriers to euphausiids that may be dwelling in the depths (Boden and Kampa, 1958). In other words, euphausiids, during their vertical migration, do not encounter the temperature difference between day and night levels that has been discussed by H. B. Moore (1952).

#### *Annual Variations in Swarming*

The statistics for annual yields of euphausiids recorded at the Onagawa fish market (Table 2) indicate remarkable annual changes in euphausiid abundance in the vicinity of Kinkazan. Each value in Table 2 can be interpreted as an index of the standing crop of swarming euphausiids in each swarming sea-

son, because there were no notable changes in fishing effort (i.e., the number of fishing boats) throughout these seven years, and almost all euphausiids fished in the area were landed at the Onagawa fish market.

Similarly, in the nearshore waters of the Sea of Japan, it was also observed that the extent of swarming fluctuates widely from year to year. Although profuse swarming occurred during the period from 1943 through 1949 (Uda, 1952), it has been observed only rarely since 1953. The relative abundance of euphausiid swarming during the period 1945–1956 in the nearshore waters of the Sea of Japan is shown in Figure 7. Each symbol represents an answer from an individual fisherman. Figure 7 illustrates that intensive swarming in the Sea of Japan took place until 1953 but ceased thereafter. Although no numerical data



TABLE 2  
ANNUAL YIELDS OF *Euphausia pacifica* FROM THE  
KINKAZAN AREA\*

YEAR	YIELD (TONS)
1953	431.8
1954	0.0
1955	887.1
1956	1,029.2
1957	274.0
1958	404.1
1959	1,419.1

\* From the statistics of the Onagawa fish market.

are available, the information at hand indicates that the disappearance of swarms from near-shore waters continued at least until 1958.

In order to relate the annual change in the euphausiid swarming to the surface water temperature, examination of water temperatures during the first six months of the year at Enoshima (Fig. 5a) are plotted in Figures 5b (1954) to 5g (1959) with 10-day intervals. Each point represents the mean values of 10 daily measurements.

Upon relating Figure 5 to Table 2, it is quite obvious that the temperature was abnormally higher than the mean throughout the winter and spring of 1954, when absolutely no euphausiids were caught. On the other hand, in 1956 and 1959, when more than 1,000 tons of euphausiids were captured, the temperature was a little lower than the mean in February and March 1956, and it was a little higher than, but close to, the mean in April and May 1959. Euphausiids were fished mainly in the early spring of 1956, while they were caught more abundantly late in the spring of 1959 than earlier (Fig. 2).

The peculiarity of the water temperature in the winter and spring months of 1954 also can be learned from Figure 8. Figure 8 is based on the monthly observations at the station 10 miles off Tsubakishima (Fig. 1a), which is located closer to Kinkazan than is Ozaki. Figure 8a shows the water temperature profile down to a depth of 200 m during the period from November 1953 to November 1954. Figure 8b shows the temperature profile at the same station for the following year. It is obvious that a remarkable temperature gradient was present during the winter and spring months of 1954, when no euphausiids were

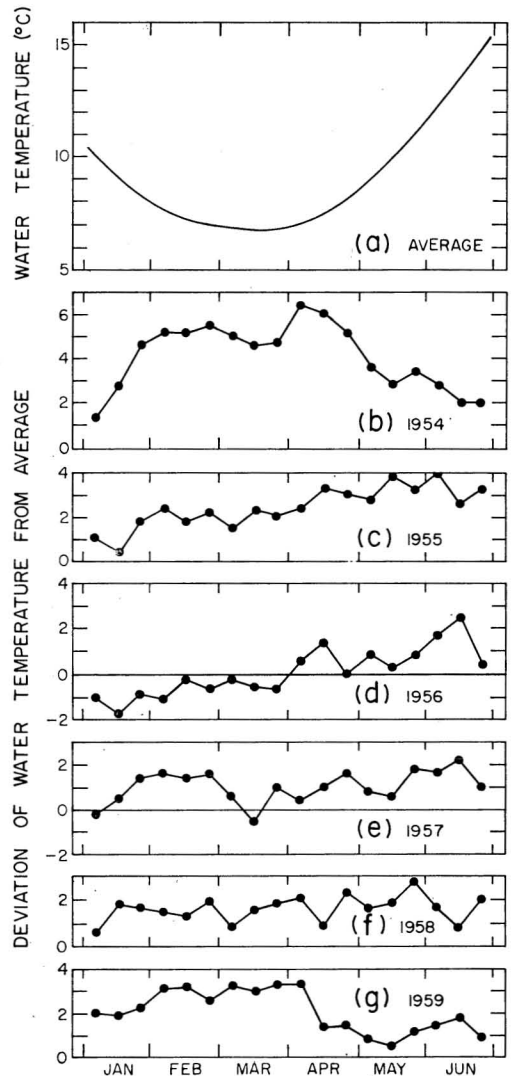


FIG. 5. Surface water temperatures at Enoshima. (a), Average temperatures for 1910-1944 and 1953-1959; (b)-(g), deviations from the mean for 1954-1959.

captured. Considerable warm water occupied the surface layers in the spring of 1954, especially in April, which corresponds to the middle of the swarming season in the Kinkazan waters. The temperature profile for the next year (Fig. 8b) shows normal seasonal change in the area, as is indicated by the temperature profiles at the stations off Ozaki and Shiroyazaki (Fig. 6).

The records of water temperatures observed



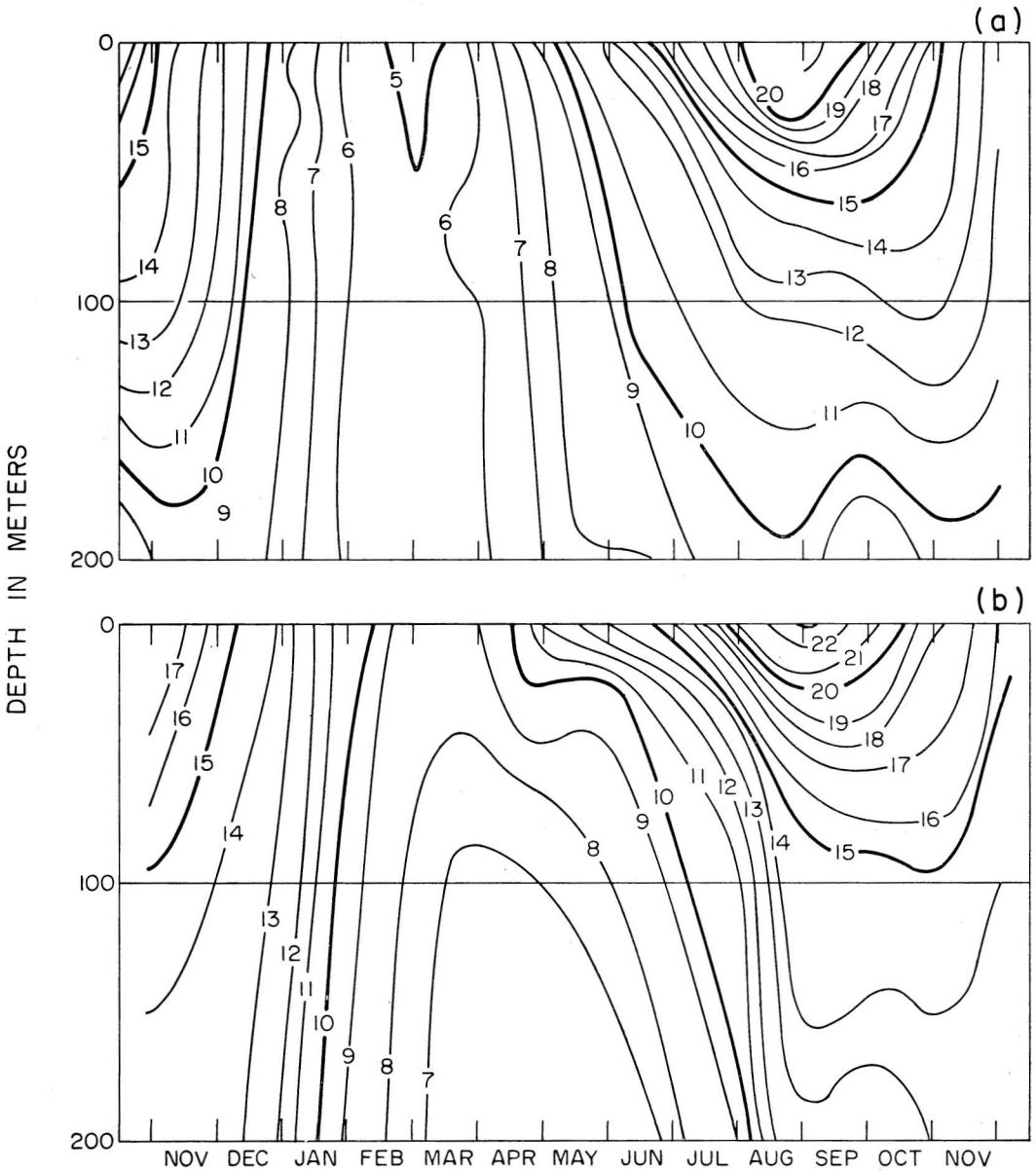


FIG. 6. Average annual changes of water temperature profile 10 miles off (a) Ozaki during 1919-1939, and (b) Shioyazaki during 1914-1939. Locations are shown in Figure 1a.

at Kyogasaki were the only data available for relating temperature to the long-term change in swarming in the Sea of Japan shown in Figure 7. The monthly mean values of water temperatures in a given month from 1943 to 1957 are plotted in Figure 9. It appears that all water temperatures in March, from 1943 to 1952, were lower than the accumulated av-

erage value calculated over the years beginning with 1915 (dashed lines in Fig. 9). March is the month when swarming takes place extensively in the Wakasawan area. Also, the least squares regressions (solid lines in Fig. 9) obtained from values during these 14 years suggest an explanation for the disappearance of euphausiids from the neritic areas. All regres-

	ZONE	YEAR											
		1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
HONSHU	2								● *	●	○		
	4			● *	*			● *		●	●○	●○	●○
	5	● *				● *			●	●○	●	●○○	●●○
	6	●	●	● *	●						○		
	7							●	●	○			
	11								○	○	○	●	●
	12								● *	●	○	○	
	15			●● *	●●● *	●●● *	●● *	●●●● *	●●●● *	●●●● *	●●○	○○○○	○○○○
	16			●	●	●	●		●●●●	●●●●	○○○○	○○○○	○○○○
	17				*			● *	○○	○○	○	●●●	●●○
	18	●		●●	●● *	*	*		●	●○	○○	●○○	●○○
	19		*	*	●●● *	●●● *	●	●● *	●●●●	●○○○	○○○○	●●○○	●●○○
	21				*		*	*	●	●	○	●●●●	●●●●
22	● **		*	*					●○○○	●○○○	●○○○	●○○○	
KYUSHU	23					●	●	●●	○	○	●○○	●○○	
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	26		**						● *	●	●	○○	○○

(1) ○ (2) ○ (3) ● (4) ● (5) ● (6) \*

FIG. 7. Fluctuation in relative abundance of *Euphausia pacifica* swarming at the surface in the coastal areas of the Sea of Japan. (1) a few, (2) less than usual, (3) usual, (4) more abundant than usual, (5) much more abundant than usual, (6) extraordinarily abundant.

sions have a positive slope, which means that successive years tended to be warmer during this period, and this tendency is greatest in March and April (Fig. 9b and c) when the most extensive swarmings take place.

#### Predators

It was learned from fishermen that there is a close relationship between the abundance of euphausiids at the sea surface and fishes in the swarming areas of euphausiids. Various previous workers—Smith (1879), Lebour (1924), MacDonald (1927), Hjort and Ruud (1929), Sheard (1953), Zelickman (1961), and Marr (1962) among others—also reported the euphausiid swarms accompanied by predators such as fishes, whales, and birds. In order to

take this relationship into account, an investigation was made on representative predators.

Figure 10 shows the change in annual yield of Japanese mackerel, *Scomber japonicus*, from the Wakasawan area. This was obtained from the statistics of the Ministry of Agriculture and Forestry. Spring mackerel fishing in the area usually is carried out during the period approximately corresponding to the swarming season of euphausiids, and examination of stomach contents of mackerel has shown that the mackerel is predatory on euphausiids. A conspicuous increase in the yield from 1945 to 1946 (Fig. 10) probably was caused by restoration of the local fishing fleet from the war-time decline, i.e., the increase of fishing effort. In 1949, when an extraordinary abundance of

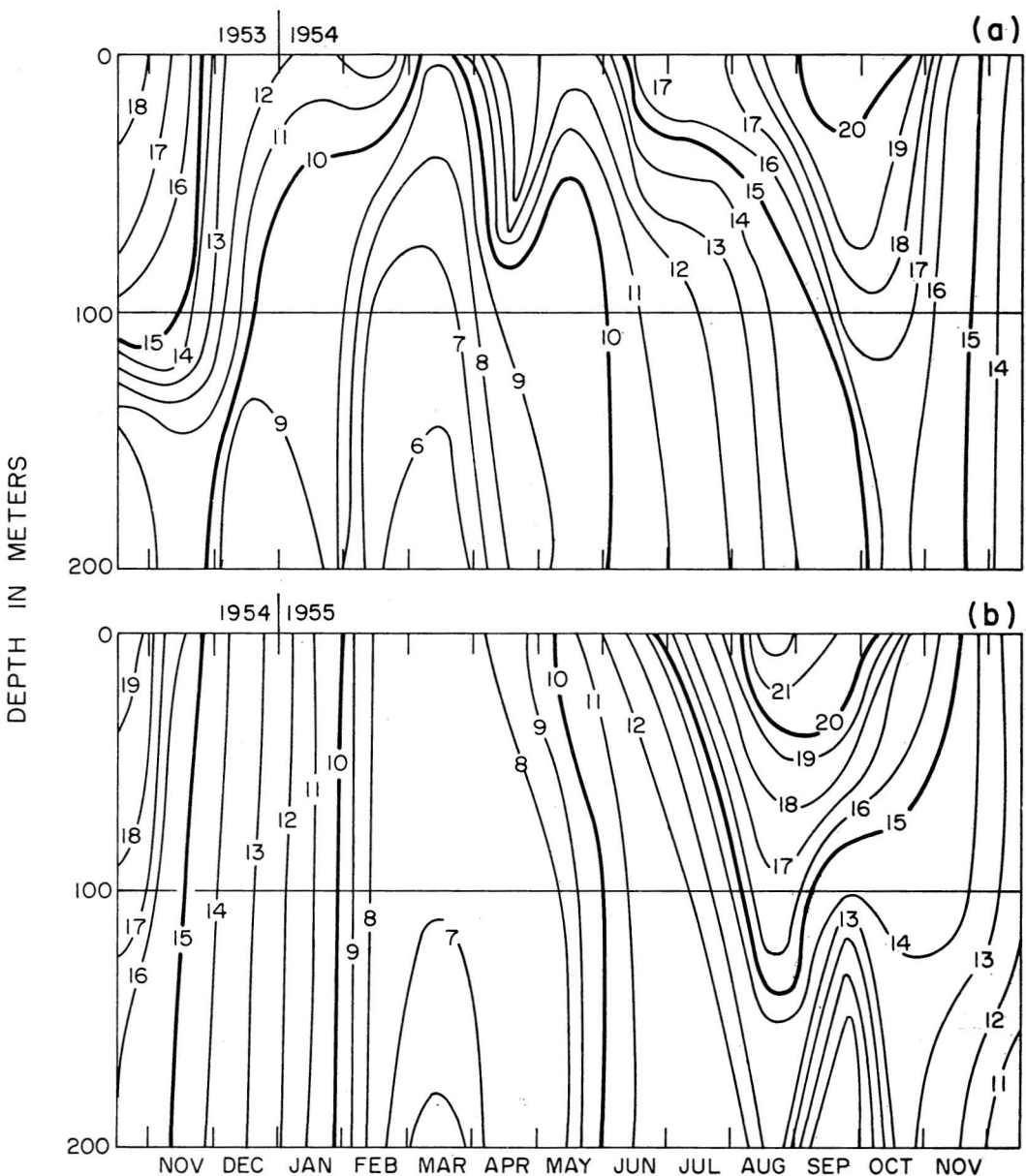


FIG. 8. Water temperature 10 miles off Tsubakishima. Location shown in Figure 1a. (a), Fall 1953 to fall 1954; (b), fall 1954 to fall 1955.

mackerel was fished, abnormally conspicuous swarming of euphausiids was observed in this area (Fig. 7). Rapid decrease in mackerel yield occurring in 1952 and thereafter may be related to the disappearance of the spring swarms of euphausiids from the coastal area after that year.

Table 3 shows the change in annual yield of sand eel, *Ammodytes personatus*, from the Kinkazan waters. In general, the fishing season of sand eel in this area starts in January and terminates by the end of July, and they are taken from almost the same area as the euphausiid fishing ground shown in Figure 1b.

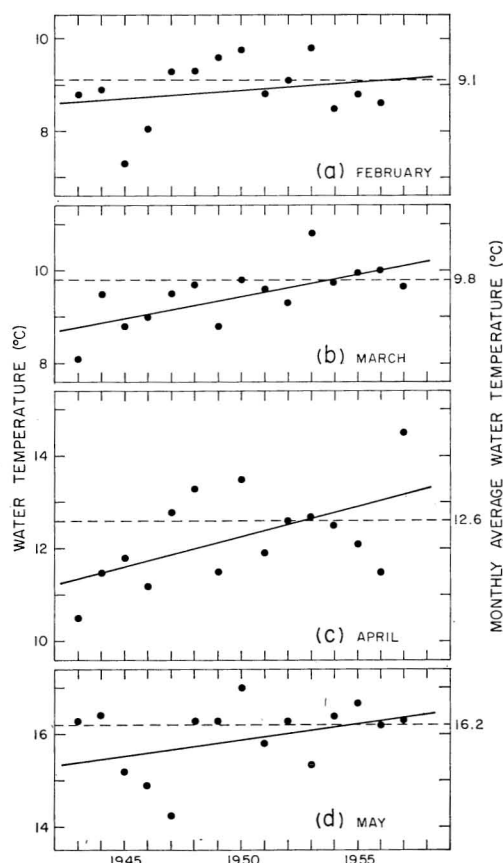


FIG. 9. Monthly mean temperature in each of four spring months from 1943 through 1957 at Kyogasaki. Dashed lines show mean temperatures, 1915-1957; solid lines show least squares regressions for 1943-1957.

Comparing Table 3 with Table 2, it is obvious that annual yields of both euphausiids and sand eel from the area fluctuate in parallel.

In addition to the sand eel, the sea gull, *Larus crassirostris*, and a small blackish bird, *Cerorhinca monocerata*, can be considered predators on euphausiids in the Kinkazan waters. According to local fishermen, *C. monocerata* can dive into the deep, and it probably attacks submerged euphausiids from the bottom and drives them up to the surface.

#### DISCUSSION

It has been clearly demonstrated here that the swarming of *Euphausia pacifica* in the nearshore waters of Japan is closely related to

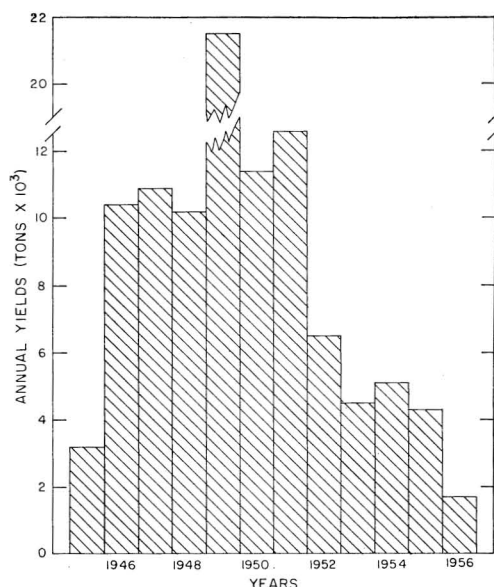


FIG. 10. Annual yield of Japanese mackerel, *Scomber japonicus*, from the Wakasawan area.

cold water temperatures. This may be expected, since the species is a boreal form, occurring commonly north of the subarctic convergence, as shown by Banner (1949), Boden et al. (1955), Nemoto (1957), Brinton (1962a), and Ponomareva (1963). The habitat is crescent in shape, covering the northern part of the North Pacific. *E. pacifica* occurs in the cold water lying under the upper strata in the Sea of Japan (Komaki and Matsue, 1958).

Inasmuch as the branches of the warm Kuroshio wash the Japanese coasts, *E. pacifica* may be excluded from the coastal areas except during the coldest season, while it is more commonly concentrated in the nearshore and inshore waters of the eastern North Pacific (Banner, 1949; Boden et al., 1955; Brinton, 1962a, b; Banse and Semon, 1963; Regan, 1963). Except during its swarming season,

TABLE 3  
ANNUAL YIELD OF SAND EEL, *Ammodytes personatus*, FROM THE KINKAZAN AREA\*

YEAR	YIELD (TONS)
1953	741.7
1954	349.6
1955	580.8
1956	4,029.1

\* From the statistics of the Onagawa fish market.

*E. pacifica* is seldom found in the stomachs of various fishes caught on the continental shelves around Japan. Therefore, the approach of the offshore populations of *E. pacifica* into near-shore waters must be the first step of swarming in the coastal area around Japan. It may be considered as a seasonal expansion of their distribution to the coastal areas, inasmuch as Beklemishev and Semina (1956) and Semina (1958) demonstrated that the seasonal change of zoo- and phytogeographical boundaries accompanied the seasonal shift of the convergence between Kuroshio and Oyashio.

The size of the approaching offshore populations may be strongly influenced by temperature conditions from year to year. Uda (1964) illustrated and discussed the meanderings of the Kuroshio. Masuzawa (1960) discussed the annual variation of the Kuroshio axis, and showed that the north-south swing of the axis around the point of 36°N, 144°E was much greater than that of the other portions, and also that there is a possibility that the isolation of the water bodies may take place at the top of the conspicuous current axis curvature. The point mentioned above is located in the southeast off Kinkazan, and therefore it is quite possible that an isolated warm water mass from the top of the northward curvature of the Kuroshio approaches the coastal region around Kinkazan in some cases. The extraordinarily high temperature observed in the winter and spring months of 1954 possibly was caused by such an approach of the isolated water mass, although Masuzawa's data of 1954 through 1959 showed that the northernmost meandering of the current axis occurred in 1955 and not in 1954.

Miyata and Shimomura (1959) and Miyata (1960) classified several cold water masses in the offshore areas of the Sea of Japan and discussed their location and transference. Uda (1952, 1958) discussed the variation of the conditions in this sea, describing the change of the position of the polar front from year to year. It cannot be doubted that the offshore cold water masses come close to the Honshu coasts in winter and spring when the monsoon blowing from Siberia prevails.

Actually, the cold water masses defined by the above workers are located off the zones

where the swarming of euphausiids takes place most actively, e.g., around Sadogashima (zone 8), in the Wakasawan area (zones 15 and 16), and around Oki (zone 21) (Fig. 1a). In winter and spring these cold water masses may protrude against the coastal areas in the manner of a tongue. The warm water of the Tsushima current is very shallow because of the shallowness (about 100 m) of the Tsushima Kaikyo. Accordingly, it is likely that the originally warm Tsushima current water will be mixed with cold water masses through relatively simple processes.

The stronger the approach of offshore cold water masses to the coast and the stronger the mixing in the coastal areas, the more profuse will be the swarmings of euphausiids along the coasts on the Sea of Japan. As a matter of fact, Uda (1958) showed that the polar front came very close to the Honshu coast during the period from 1946 to 1949, while it was away from the coast after 1952. It appears that such approach and recession of the polar front corresponds in time to the change in swarming (Fig. 7).

Thus, low temperature induces the coastward approach of the offshore stocks of *E. pacifica*, and it must be one of the indispensable conditions for surface swarming in Japanese near-shore areas. However, it would be premature to conclude that it is the only sufficient condition. One is still unable to explain why euphausiids do not swarm in early and middle winter months when the temperature is as low as it is in spring and vertical mixing is actively taking place, and why they come to the surface in the daytime when the light intensity may be harmful to them.

There have been several different opinions as to the cause of the daytime surface-swarming of euphausiids: (a) Predators may drive euphausiids to the surface, as previously mentioned. (b) Euphausiids come to the surface to search for food in the upper strata where phytoplankton is abundant (Paulsen, 1909; Manteufel, 1938, 1941). (c) Current conditions may accumulate euphausiids, or stimulate them to swarm at the surface (Fish and Johnson, 1937; Einarsson, 1945; Peters, 1955). (d) Some internal demands related to maturation or reproduction may drive euphausiids

to the sea surface (Sheard, 1953; Ponomareva, 1959, 1963; Zelickman, 1961). Although these theories are still controversial, the last can probably be applied to the swarming of *E. pacifica* in Japanese nearshore waters.

The author observed that more than 50% of the females in a few swarms in the Sea of Japan had spermatophores in the thelycum. No specimens from the Kinkazan area were carrying spermatophores. However, the females were full-grown and the degree of maturation of the ovaries corresponded to the stage 3 defined by Ruud (1932) or to the stage 5 or 6 established by Bargmann (1945) for *Euphausia superba*. As is shown in Figure 2, offshore populations of *E. pacifica* seem to come close to the coast around Kinkazan with a pulseline rhythm. This may suggest that the population of *E. pacifica* can be divided into several stocks in accordance with the phase of maturation, and that, as stocks reach a certain degree of maturity, they approach the coast in succession. The tendency for swarming to occur earlier in the southern part of the Sea of Japan than in the northern part, as shown in Figure 3, may be understood in relation to the geographical difference between the maturing or reproduction phases of euphausiids and to seasonal differences in temperature of the two areas.

Kun's opinion (1955) on the daytime ascent of *Calanus tonsus*, which may be related to a biochemical process (e.g., transformation of vegetable carotenoids into vitamin A by ultraviolet radiation) may be applied to the swarming of euphausiids. During certain periods of their maturing or reproductive process, euphausiids might need rather strong daylight, regardless of the usual daytime level of their vertical distribution. As listed in Table 1, nearly all species whose swarming has been reported hitherto are cold water forms. This suggests that their physiology should be analyzed, with the objective of solving the mechanism of this peculiar behavior of euphausiids.

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#### REFERENCES

- BANNER, A. H. 1949. A taxonomic study of the Mysidacea and Euphausiacea (Crustacea) of the northeastern Pacific, Part III. Euphausiacea. Trans. Roy. Can. Inst. 28: 1-63.
- BANSE, K., and D. SEMON. 1963. On the effective cross-section of the Isaacs-Kidd mid-water trawl. Univ. Washington Dept. Oceanogr. Tech. Rept. 88:1-9.
- BARGMANN, H. E. 1945. The development and life history of adolescent and adult krill, *Euphausia superba*. Discovery Rept. 23: 103-176.
- BEKLEMISHEV, K. V., and G. I. SEMINA. 1956. On the structure of the biogeographical boundary between the boreal and tropical regions of the pelagial of the northwestern Pacific Ocean. [In Russian.] Dokl. Acad. Nauk SSSR 108(6):1057-1060.
- BIGELOW, H. B. 1926. Plankton of the offshore water of the Gulf of Maine. Bull. Bur. Fish. Washington 40(2):1-486.
- BODEN, B. P., M. W. JOHNSON, and E. BRINTON. 1955. The Euphausiacea (Crustacea) of the North Pacific. Bull. Scripps Inst. Oceanogr. 6(8):287-400.
- and E. M. KAMPA. 1958. Lumière bioluminescence et migrations de la couche diffusante profonde en Méditerranée occidentale. Vie Milieu 9(1):1-10.
- BRINTON, E. 1962a. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. New Ser. 8(2):51-218.
- 1962b. Variable factors affecting the apparent range and estimated concentration of euphausiids in the North Pacific. Pacific Sci. 16(4):374-408.
- DAKIN, W. J., and A. N. COLEFAX. 1940. The plankton of the Australian coastal waters off New South Wales, Part I. Publications of University of Sydney, Department of Zoology, Monograph 1:1-215.



- EINARSSON, H. 1945. Euphausiacea, I. North Atlantic species. *Dana Rept.* 27:1-185.
- FISH, C. J., and M. W. JOHNSON. 1937. The biology and zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *J. Biol. Bd. Canada* 3(3):189-322.
- FISHER, F. S., S. K. KON, and S. Y. THOMPSON. 1953. Vitamin A and carotenoids in some Mediterranean Crustacea with a note on the swarming of *Meganyctiphanes*. *Bull. Inst. Oceanogr. Monaco* 1021:1-19.
- FRASER, F. S. 1936. On the development and distribution of the young stages of krill (*Euphausia superba*). *Discovery Rept.* 14:1-192.
- GUNTHER, E. R. 1949. The habit of fin whales. *Discovery Rept.* 25:113-142.
- HANSEN, H. J. 1916. The euphausiacean crustaceans of the Albatross expeditions to the Philippines. *Proc. U. S. Natl. Mus.* 49: 635-654.
- HARDY, A. C., and E. R. GUNTHER. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. *Discovery Rept.* 11:1-456.
- HJORD, J., and J. T. RUUD. 1929. Whaling and fishing in the North Atlantic. *Rapp. P.-v. Réun. Cons. Perm. Intern. Explor. Mer* 56:1-123.
- KOMAKI, Y. 1957. On the "esada" (*Euphausia pacifica* H. J. Hansen) fishery in the vicinity of the Ojika Peninsula. [In Japanese.] *Information Bull. Whales Research Inst.* 60: 10-17.
- and Y. MATSUE. 1958. Ecological studies on the Euphausiacea distributing in the Sea of Japan. [In Japanese.] *Report of Cooperative Survey of the Warm Tsushima Current and Related Waters* 2:146-162.
- KUN, M. S. 1955. About reasons of various behaviour of mackerel. [In Russian.] *Trudy Tikhookean. Inst. Morsk. Ryb. Khoz. okeanogr.* 43:206-208.
- LEBOUR, M. V. 1924. The Euphausiidae in the neighbourhood of Plymouth and their importance as herring food. *J. Mar. Biol. Assoc. U.K.* 13(2):402-418.
- LO BIANCO, S. 1902. Le pesche pelagiche eseguite dal Maia nelle vicinanze di Capri. *Mitt. Zool. Stn. Neapel* 15:413-482.
- 1903. Le pesche abissali da F. A. Krupp col yacht Puritan nelle adiacenze di Capri ed in altra località del Medditerraneo. *Mitt. Zool. Stn. Neapel* 16:109-279.
- MACDONALD, R. 1927. Food and habits of *Meganyctiphanes norvegica*. *J. Mar. Biol. Assoc. U.K.* 14(3):753-784.
- MANTEUFEL, B. P. 1938. A short essay on changes of plankton in the Barents Sea. [In Russian with English summary.] *Trudy Polar. Inst. Morsk. Ryb. Khoz. Okeanogr.* 1:134-148.
- 1941. Plankton and herring in the Barents Sea. [In Russian with English summary.] *Ibid.* 7:125-216.
- MARR, J. W. S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Rept.* 32:33-464.
- MASUZAWA, J. 1960. Statistical characteristics of the Kuroshio current. *Oceanogr. Mag.* 12(1):7-15.
- MIYATA, K. 1960. Hydrographic characteristics of the polar front fishing grounds in the western part of the Sea of Japan (August-September, 1959). [In Japanese.] *Report on the Polar Front Fishing Ground in the Sea of Japan, 1959*, pp. 135-151.
- and T. SHIMOMURA. 1959. On the transfers of low temperature regions in the north Japan Sea in spring. [In Japanese with English summary.] *Bull. Japan Sea Regional Fish. Res. Lab.* 7:1-16.
- MOORE, H. B. 1952. Physical factors affecting the distribution of euphausiids in the North Atlantic. *Bull. Mar. Sci. Gulf Caribb.* 1(4):278-305.
- MOORE, H. F. 1898. Observations on the herring and herring fisheries of the coast, with special reference to the vicinity of Passamaquoddy Bay. *Rept. U. S. Fish. Comm.* 1896, pp. 387-442.
- MOSENTZOVA, T. N. 1939. The seasonal changes in the macroplankton in Barents Sea (based on materials collected in 1938). [In Russian with English summary.] *Trudy Polar. Inst. Morsk. Ryb. Khoz. Okeanogr.* 4:129-147.
- MURRAY, J. 1888. On the effects of winds on the distribution of temperature in the sea and fresh-water lochs of the west of Scotland. *Scot. Geogr. Mag.* 4:345-365.



- NEMOTO, T. 1957. Foods of baleen whales in the northern Pacific. Sci. Rept. Whales Res. Inst., Tokyo 12:33-89.
- PAULSEN, O. 1909. Plankton investigations in the waters around Iceland and in the North Atlantic in 1904. Meddr. Kommn Havunders., Serie: Plankton 1(8):1-57.
- PETERS, H. 1955. Über das Vorkommen des Walkrebschens *Euphausia superba* Dana und seine Bedeutung für die Ernährung des südlichen Baren Wale. [English summary.] Arch. Fisch.-wiss. 6(5,6):288-304.
- PONOMAREVA, L. A. 1955. Nutrition and distribution of euphausiids in the Sea of Japan. [In Russian.] Zool. Z. 34:85-98.
- 1959. Reproduction of Euphausiidae of the Sea of Japan and development of their early larval stages. [In Russian.] Ibid. 38(11):1643-1662.
- 1963. The euphausiids of the North Pacific, their distribution and mass species. [In Russian with English summary.] Inst. Oceanol. Acad. Sci. U.S.S.R., Moscow, Monogr.:1-142.
- REGAN, L. 1963. Field trials with the Clarke-Bumpus plankton sampler. Inst. Oceanogr., Univ. British Columbia, Manuscript Rept. 16:1-28.
- RUUD, J. T. 1932. On the biology of southern Euphausiidae. Hvalråd. Skr. 2:1-105.
- SEMINA, G. I. 1958. Relation between phyto-geographic zones in the pelagial of the north-western part of the Pacific Ocean with the distribution of water masses in the region. [In Russian.] Trudy Inst. Okeanol. 27:66-76.
- SHEARD, K. 1953. Taxonomy, distribution and development of the Euphausiacea (Crustacea). British-Australian-New Zealand Research Exped. Rept., Ser. B, 8(1):1-72.
- SMITH, S. I. 1879. The stalk-eyed crustaceans of the Atlantic coast of North America, north of Cape Cod. Trans. Connecticut Acad. Arts Sci. 5:27-138.
- TATTERSALL, W. M. 1936. Mysidacea and Euphausiacea. Sci. Rept. Barrier Reef Exped. 5(4):143-176.
- UDA, M. 1952. On the hydrographical fluctuation in the Japan Sea (preliminary report). Appendix: The extraordinary abundant catch of *Euphausia pacifica* Hansen in winter and spring of 1948 along the coast of the Japan Sea. [In Japanese with English summary.] Japan Sea Regional Fish. Res. Lab., Spec. Publ. for its Third Anniversary of Foundation, pp. 291-300.
- 1958. On the out-lined sea conditions of the Sea of Japan. [In Japanese.] Reports of the Cooperative Survey of the Warm Tsushima Current and Related Waters 1:31-45.
- 1964. On the nature of the Kuroshio, its origin and meanders, pp. 98-107. In: K. Yoshida, ed., Studies on Oceanography. Tokyo.
- ZELICKMAN, E. A. 1961. The behavior pattern of the Barents Sea Euphausiacea and possible causes of seasonal vertical migrations. Intern. Revue Ges. Hydrobiol. 46(2):276-281.